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ADULT BODY SIZE AND SURVIVORSHIP IN A FIELD POPULATION OF *AEDES TRISERIATUS*[1]

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ABSTRACT. *Aedes triseriatus* pupae, host-seeking, and ovipositing females were collected at a southern Wisconsin site endemic for La Crosse encephalitis virus. The host-seeking and ovipositing females were age-graded by the Detinova and Polovodova techniques, respectively. Wing lengths were determined for all mosquitoes. Wing lengths of the mosquitoes collected as pupae were predicted from pupal weight by a simple regression equation. There was significant seasonal variation in body size of adult females, but no strong evidence that increased size was advantageous to survival. It is concluded therefore that the potential length of infective life is not affected by the size of the adult female.

INTRODUCTION

The relationship between adult body size and vector capability of female mosquitoes has attracted increasing attention by researchers. Size may influence vectorial capacity by: 1) affecting life table parameters and/or 2) affecting the ability of the mosquito to become infected and to transmit a pathogen. Large size was experimentally linked to increased survival rates in *Aedes triseriatus* (Say) and *Culex tarsalis* Coquillett by McCombs (1980)[2] and Reisen et al. (1984), respectively. Until recently, however, field studies of this relationship were generally lacking. Hawley (1985) reported that, in general, larger adult *Ae. sierrensis* (Ludlow) females lived longer than smaller ones. Haramis (1983) noted increased parity rates among large *Ae. triseriatus* compared with those of small ones and suggested that these rates indicated longer survival or increased bloodfeeding success with increased size. Similarly, Nasci (1986a) reported increased parity rates with increasing size in 3 floodwater species, *Psorophora columbiae* (Dyar and Knab), *Ae. atlanticus* (Dyar and Knab), and *Ae. vexans* (Meigen), and one permanent water species, *Cx. salinarius* Coq. In a more extensive field study of *Ae. aegypti* (Linn.) in a Louisiana tire yard, Nasci (1986b) obtained similar results. The average wing length of adults reared from field-collected pupae was significantly less than that of host-seeking nulliparous individuals, which, in turn, was significantly less than that of host-seeking parous females. These results suggest increased fitness with increased adult body size. In a mark-release-recapture experiment involving both medium-sized and large *Ae. triseriatus* and *Ae. hendersoni* Cockerell, Walker et al. (1987) found no effect of size on daily survivorship; however, due to rearing difficulties, they were unable to investigate this relationship in small mosquitoes.

A trend toward enhanced transmission rates in relatively small mosquitoes has been reported for a number of virus-mosquito relationships. Grimstad and Haramis (1984) reported increased oral transmission rates of La Crosse (LAC) virus by small *Ae. triseriatus* mosquitoes. Patrican and DeFoliart (1985) confirmed these findings and demonstrated higher transovarial transmission rates in small *Ae. triseriatus* mosquitoes. Baqar et al. (1980) similarly noted decreasing infection rates of West Nile virus with increasing size of *Cx. tritaeniorhynchus* Giles, although the differences were not statistically significant. Takahashi (1976) found that when *Cx. tritaeniorhynchus* were reared under different nutritional regimes, well-fed larvae yielded larger adults that secreted Japanese encephalitis virus at a reduced rate.

The objectives in our studies were to determine: 1) the size range of adult *Ae. triseriatus* females in the field, 2) whether the size range changes throughout the season, 3) if increased size confers an increased probability of survival and successful completion of the various physiological events in the life of an adult female, and 4) if vector size is an important factor in the epidemiology of LAC virus.

MATERIALS AND METHODS

Mosquito collections. Ovipositing mosquitoes were collected on the R.P. and M.G. Hanson

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[2] McCombs, S. D. 1980. Effect of differential nutrition of larvae on adult fitness of *Aedes triseriatus*. M.S. Thesis. University of Notre Dame. 123 pp.

farm in south-central Wisconsin (Iowa Co.) using the female-retaining trap described by Landry and DeFoliart (1987). These collections were made throughout the field seasons of 1982 through 1985.

Host-seeking mosquitoes were collected in 1985 using the trap described by Landry and DeFoliart (1986), and in 1986, with this trap following removal of the plastic crisper and lowering of the circular cover. Carbon dioxide, released at a flow rate of approximately 1.0 liter/min from pressurized cylinders, was the attractant. Six traps were operated initially, but after 3½ weeks the 2 least productive traps were removed. The trapped mosquitoes were collected daily from June 20 through October 13, except for one week, when the traps were not in operation because of a lack of CO_2.

A census of 10 tree holes on the Hanson farm was conducted from April 24 to October 8, 1986. During July, August and September, the tree holes were checked twice weekly; the remainder of the time they were checked weekly. The tree holes were completely emptied and usually rinsed with a portion of the collected water. The entire contents were brought back to the laboratory, where the larvae and pupae were counted. The pupae were blotted on a paper towel and weighed; the larvae and the water were returned to their original tree holes. Adults were allowed to emerge from the pupae in small containers attached to the trees near the tree holes.

Determination of size of emerging females. Pupal weights were transformed to predicted wing lengths for emerging females using the equation: wing length = 2.21 + 0.0329 (pupal weight), (R^2 = 0.835; $P < 0.005$). Pupal weights were in milligrams and wings were measured in millimeters from the axillary incision to the apical margin, excluding the fringe scales. This equation was calculated from wing measurements of a sample of 56 females which emerged in our laboratory from pupae collected in the field.

Dissections and measurements. Parity of mosquitoes collected in CO_2 traps was determined by removing ovaries in a drop of mosquito saline (Hayes 1953) and observing tracheoles with a compound microscope (×250) (Detinova 1962). Dissection of ovipositing mosquitoes was explained by Landry and DeFoliart (1987).

Wing lengths of mosquitoes were measured using a dissecting microscope with an ocular micrometer. Mosquitoes that had both wings frayed were not tabulated. Individuals for which parity or the number of gonotrophic cycles could not be determined, but whose wings were measured, are included in the not determined category in Table 1. Mosquitoes were divided into 3 size groups: 1) small: females with wing length ≤ 2.90 mm; 2) medium: wing length from 2.91 to 3.65 mm; and 3) large: wing length > 3.65 mm. To detect subtle trends in survivorship, the host-seeking females of each year were further sorted by wing length into 11 size classes. Except for one size class which was 0.2 mm in range size classes were 0.1 gradations from 2.8 mm to 3.8 mm, with two additional classes being <2.80 mm and >3.80 mm. This yielded approximately 200 females per size class. In analyzing changes in wing length during the season, wing length and Julian date of capture for the nulliparous and uniparous females were used for the host-seeking and ovipositing females, respectively.

To allow for the comparison of our data with previously published results, the wing measurements that were made from the axillary incision to the apical margin (wgl-a) were transformed to correspond to measurements made from the base of the costal vein to the apical margin (wgl-c) using the regression equation: wgl-a = 0.0944 + 0.880 (wgl-c). (R^2 = 0.991; $P < 0.005$). In addition, wing lengths (wgl-c) were transformed to dry body weight using the equation of McCombs (Fish 1985): dry weight = 0.009 $(\text{wgl-c})^3$ − 0.017.

The coefficient of variation (CV) was calculated on values converted to dry weights by: CV = (standard deviation) × (100)/mean.

Determination of survival rates. The parous rate was used to determine the survival rates. According to Service (1976), the parous rate is equal to the survivorship per gonotrophic cycle provided that recruitment into the population being sampled is constant, or in the case of a seasonal mosquito such as *Ae. triseriatus* in southern Wisconsin, that the population is sampled from the onset of emergence to the end of emergence. This criterion was met by sampling virtually from the time that host-seeking individuals first appeared until the end of the season (when collections of host-seeking mosquitoes diminished to less than 0.25 females per trap per day).

Determination of bloodfeeding success. The relationship between size and bloodfeeding success was examined by comparing the distribution of the wing lengths of the partially engorged host-seeking females collected in 1986 to the unengorged females collected in the same year. The wing lengths were divided into 14 size classes and tested for independence with a 2 × 14 contingency table.

Data analysis. The average wing lengths for the yearly collections were compared by analysis of variance and the Student's *t* test (Table 1). Significant seasonal changes were determined by Student's *t* test using two weekly averages, at least one month apart. The relationship between size and survivorship was tested using a 2 × 11 Chi-square contingency table. The vari-

Table 1. Wing lengths of female *Aedes triseriatus* collected in Iowa Co., Wisconsin, 1982–86.

Physiological age	Number	Mean wing length (mm)	Range (mm)	Coefficient of variation
Emerging (1986)	395	3.47 (0.34)[1]	2.64–4.41	31.52
Host-seeking				
1985				
Nulliparous	384	3.19[2a] (0.31)	2.32–4.05	51.42
Parous	384	3.22[a] (0.31)	2.40–4.12	50.91
Not determined	76	3.28 (0.33)	2.70–3.98	
1986				
Nulliparous	592	3.36[b] (0.36)	2.55–4.28	49.29
Parous	1,082	3.29[c] (0.33)	2.40–4.20	49.72
Not determined	240	3.26 (0.33)	2.48–4.12	
Totals				
1985	844	3.21[d] (0.31)	2.32–4.12	51.16
1986	1,914	3.30[e] (0.34)	2.40–4.28	50.00
Ovipositing				
1982				
Uniparous	126	3.19[f] (0.32)	2.18–3.90	52.50
Biparous	6	3.19[f] (0.27)	2.92–3.60	46.35
Triparous	3	3.43[f] (0.16)	3.30–3.60	21.85
>Triparous	1	2.95 (NA)[3]	(NA)	(NA)
1983				
Uniparous	266	3.16[g] (0.32)	2.40–4.20	56.78
Biparous	26	3.08[g] (0.34)	2.55–3.75	62.44
Triparous	8	3.28[g] (0.26)	2.85–3.75	40.37
>Triparous	1	3.15 (NA)	(NA)	(NA)
1984				
Uniparous	618	3.36[h] (0.36)	2.48–4.42	51.51
Biparous	129	3.38[h] (0.32)	2.70–4.28	48.41
Triparous	20	3.34[h] (0.26)	2.92–3.82	38.10
>Triparous	6	3.66[h] (0.46)	3.00–3.00	47.61
1985				
Uniparous	245	3.23[i] (0.33)	2.40–4.12	52.54
Biparous	35	3.38[j] (0.32)	2.78–4.20	45.08
Triparous	1	3.00 (NA)	(NA)	(NA)
>Triparous	1	3.15 (NA)	(NA)	(NA)

[1] Mean (standard deviation).
[2] Means with different letters are significantly different:
a $t = -0.99$, df = 766, $P = 0.32$
b,c $t = 3.69$, df = 1155, $P = 0.0002$
d,e $t = -7.46$, df = 1768, $P < 0.0001$
f $f_2 = 0.81$, df = 134, $P > 0.10$
g $f_2 = 1.43$, df = 299, $P > 0.10$
h $f_3 = 1.02$, df = 776, $P > 0.10$
i,j $t = -14.74$, df = 35, $P < 0.0001$
[3] Not applicable.

ances were tested for equality using Bartlett's test for equal variance. Parity rates for 1985 and 1986 were compared using a Chi-square contingency table. The results of pair-wise Chi-square comparisons of the parous rates are shown in Table 2. Significance was assigned using a Bonferroni correction of 0.05 divided by the number of comparisons made.

RESULTS AND DISCUSSION

Size range. A total of 973 pupae were collected and weighed during 1986, of which 395 were females. Wing lengths were obtained for 2,759 host-seeking females collected during 1985 and 1986. A total of 1,694 ovipositing mosquitoes were collected from 1982 to 1985. The wing lengths of females varied widely, by more than 100%. The range of wing lengths for emerging females was calculated to be 2.64–4.41 mm; those of host-seeking females ranged from 2.32 to 4.28 mm; and wing lengths of ovipositing females varied from 2.18 to 4.42 mm (Table 1).

In field studies by various investigators to date, the size and size range of *Ae. triseriatus* (as measured by wing length) have been fairly consistent (Table 3). In an analysis of the size range of 10 mosquito species collected in light traps in New Jersey (Fish 1985), the weight of *Ae. triseriatus* was well within the range ob-

Table 2. Wing lengths and parous rates for host-seeking *Aedes triseriatus* collected in Iowa Co., Wisconsin.

	Wing length (mm)			Statistical results		
	Small (≤2.90)	Medium (2.90 < × ≤ 3.65)	Large (>3.65)	χ^2_2	*P*	
1985						
Entire year						
Number collected	102	601	66			
Parous rate	0.500	0.500	0.470	0.21	>0.10	NS*
September only						
Number collected	48	240	40			
Parous rate	0.479[a]	0.529[b]	0.300[c]	7.25	<0.05	S◇
1986						
Entire year						
Number collected	193	1,171	310			
Parous rate	0.668[d]	0.667[e]	0.555[f]	14.43	<0.005	S
September only						
Number collected	55	281	35			
Parous rate	0.727	0.829	0.743	4.96	>0.05	NS
Totals 1985 and 1986						
Number collected	295	1,772	376			
Parous rate	0.610	0.612	0.540	6.80	>0.05	NS

* Not significantly different.
◇ Significantly different.
Results of paired comparisons:
ab $\chi^2 = 0.40$, df = 1, $P = 0.527$, NS
ac $\chi^2 = 2.92$, df = 1, $P = 0.088$, NS
bc $\chi^2 = 7.20$, df = 1, $P = 0.008$, S
de $\chi^2 = 0.10$, df = 1, $P = 0.752$, NS
df $\chi^2 = 7.63$, df = 1, $P = 0.006$ S
ef $\chi^2 = 13.43$, df = 1, $P < 0.001$ S

Table 3. Reported wing lengths for field-collected *Aedes triseriatus* females.

Author (Year) and Source of collections (life stage)	Month of collection	Mean wing length (Wgl-A)[a] (mm)
Fish (1985)		
Light trap (adults)	NR[b]	3.31
Haramis (1983)		
Battery aspirator (adults)	September	3.21
Haramis (1985)		
Tree holes (pupae)	May-June	3.53
	July-August	3.52
Shaded tires (pupae)	May-June	3.38
	July-August	3.22
Mather (1983)		
NR	NR	3.27
McCombs (in Haramis 1985)		
Tree holes (pupae)	NR	3.35
Walker et al. (1987)		
Battery aspirator (adults)	July-September	3.19

[a] All necessary conversions made.
[b] NR—Not reported.

served in our study. He reported a range of approximately 0.1–1.0 mg, compared to our 0.104–1.06 mg (dry weight). He also reported coefficients of variation of 36.89 and 29.50, which were generally less than our values from 21.85 to 62.44. Haramis (1983, 1984), in 2 studies of *Ae. triseriatus* in northern Indiana, found that in September 1981, females mechanically aspirated from the understory bordering a salvage yard ranged in size from 2.51 to 4.04 mm (transformed to our method of wing measurement). Females from pupae collected at the same site throughout the following year ranged in size from 2.30 to 4.18 mm (after transformation). These values are well within the range we observed at our field site (Table 1).

Seasonal size variation. At our study site, it appears that the mean size of emerging, host-

seeking and ovipositing *Ae. triseriatus* decreased as the season progressed. In most collections, this decrease was followed by an increase in size later in the season (Fig. 1). In all cases, the collections were dominated by large and medium-sized females (Fig. 2). Peak collections of small individuals occurred in the middle of the season (Fig. 2).

Hawley (1985) noted a seasonal change in the average size of nulliparous *Ae. sierrensis* females similar to that depicted in our data for ovipositing, host-seeking, and emerging females (Fig. 1). Bock and Milby (1981) reported that the average body size of *Cx. tarsalis* females decreased during the first 2 months of the season and then gradually increased during the final 2 months. Haramis (1984) reported a seasonal decrease in the size of *Ae. triseriatus* males collected as pupae from shaded tires and tree holes and in the size of females of the same species collected from shaded tires. He failed, however, to find a significant decrease in the size of females collected from tree holes (Table 3). It thus appears that for mosquito populations studied to date, there is initially a general decrease in adult female size as a season progresses. This decrease may or may not be followed by an increase in the average size later in the season. This seasonal size variation presumably results from: 1) changes in quality of the larval environment, i.e., increased temperature, larval density, food quality and availability, production of growth retardants, accumulation of metabolites, and age structure of the resident population (Fish and Carpenter 1982, Reisen and Emory 1977, Livdahl 1982, and Carpenter 1983) and/or 2) genetic factors (Livdahl and Koenekoop 1985).

The mean size of females in each group, i.e., emerging, host-seeking, and ovipositing, varied significantly at one or more points during each season (P in all cases < 0.05) (Fig. 1). Our data also indicate a significant yearly fluctuation in wing length (Table 1) and survival rate (chi-square value = 47.00, df = 1, $P < 0.0005$). In 1985, survival rates were low and mean wing lengths were short. The following year, the average wing length of host-seeking females was significantly longer and the survival rate significantly higher. Thus, to accurately analyze the role of size in population systems, collections must be made throughout the entire season, and probably for more than one season.

Size and survivorship. Analysis of the parity rates of small, medium, and large *Ae. triseriatus* failed to show an increased parity rate with increased size. In 1985, the rates for small, medium, and large mosquitoes were not significantly different for the year as a whole (Table 2). In order to compare results with Haramis (1983), the collection made during the last week of August and all of September (the time span of his data collections) were analyzed separately. In 1985, there was a significant reduction in the parous rate of large females during this time

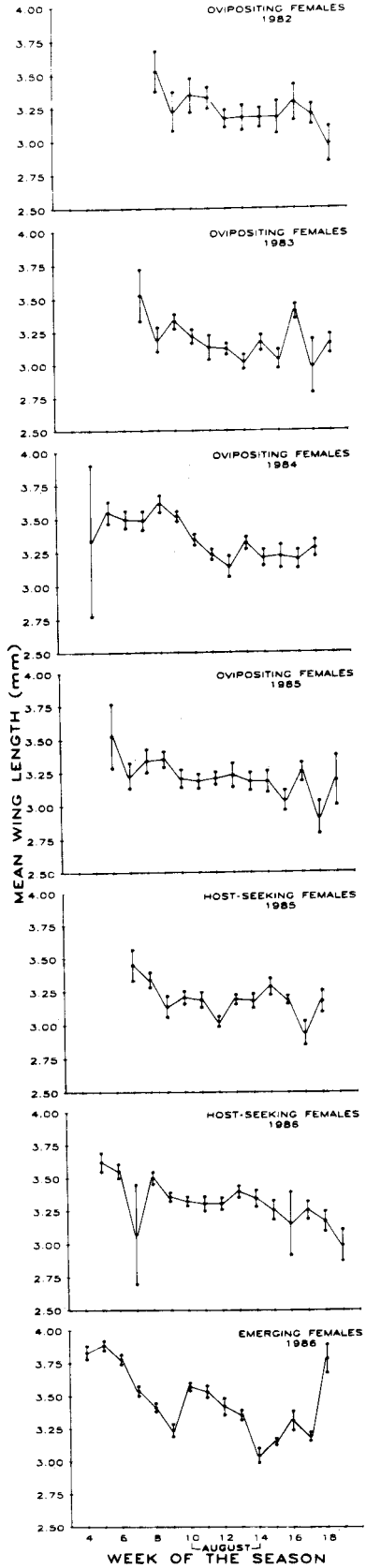

Fig. 1. Seasonal variation in winglength of female *Aedes triseriatus* collected in Iowa Co. WI. (mean ± SE).

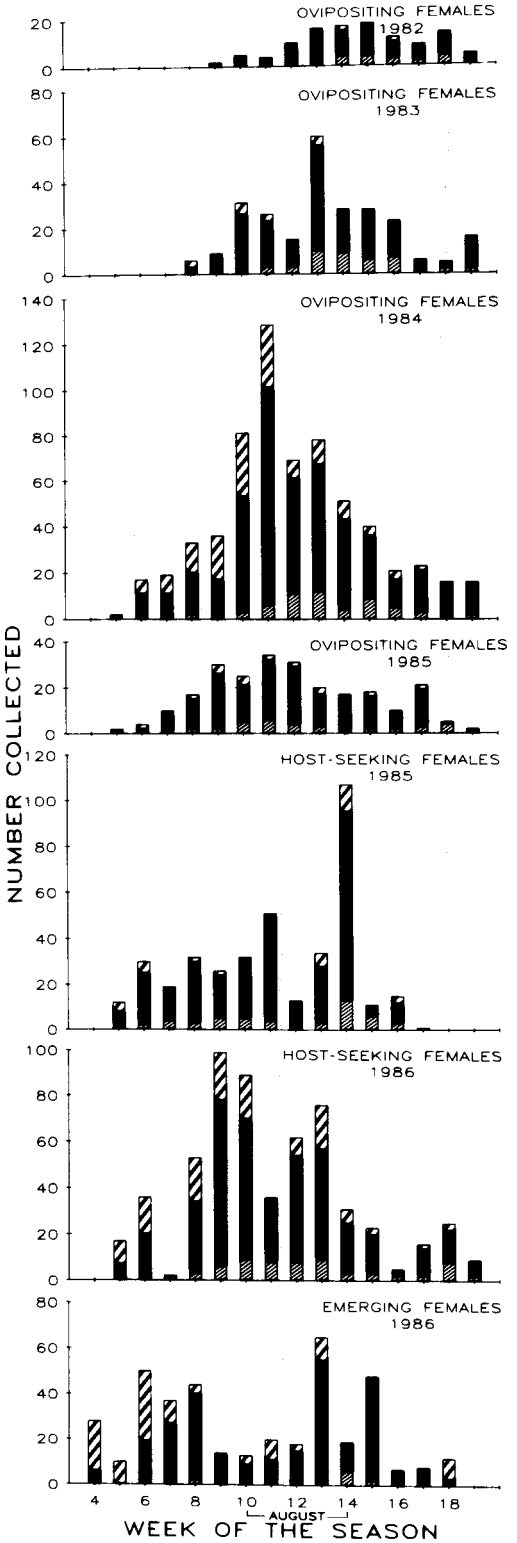

Fig. 2. Seasonal variation in the number of small (<2.90 mm) ▨ medium (2.90 ≤ × ≤ 3.65) ■ and large (>3.65 mm) ▨ sized *Aedes triseriatus* collected in Iowa Co. WI.

period. In 1986, there was also a significantly lower seasonal parous rate for the large-sized females, though no significant difference was found when the data were analyzed for the September period only (Table 2). In contrast, Haramis (1983) found that significantly more large gonoactive females were gravid or parous than were smaller females. He suggested that the higher parity rate might be attributed to: 1) a greater survival rate of large mosquitoes, whereby parous individuals accumulate at a greater rate or 2) a greater success of larger mosquitoes in obtaining a blood meal. He also reported (1985) that, in a mark-release-recapture study involving 2 size classes of female *Ae. triseriatus*, 60% of the recaptured normal-sized mosquitoes were parous while significantly fewer—40% of the small-sized females—were parous upon recapture. He offered 2 explanations: 1) an increase in size confers an increased probability of completing a gonotrophic cycle or 2) an increase in size confers an increase in survival rates.

Nasci (1986a) found that parous females of 2 of the 4 species that he examined had significantly longer wing lengths than did nulliparous females of the same species. He, too, divided his samples into size classes and found that, in all cases, the parity rate decreased concurrently with decreases in the size of the females. He concluded that large-bodied mosquitoes are more successful in obtaining a blood meal.

In our study, the relationship between size and survivorship was also examined by dividing the host-seeking females into size classes, a total of eleven, and then calculating the survivorship (parous rate) for each class. Again, no indication of increased survivorship with increasing size was found. Survivorship was found to be independent of size (chi-square value = 7.28, df = 10, $P > 0.25$) in 1985 (Fig. 3). In 1986, larger females had diminished survivorship (Fig. 3), and the relationship was significant (chi-square value = 25.22, df = 10, $P < 0.005$).

Hawley (1985), studying *Ae. sierrensis*, found a curvilinear relationship between adult size and survivorship. For 9 of his 10 size classes, an increase in size correlated with increased survivorship as measured by parous rate; however, females of the largest-sized class had a reduced survivorship.

In contrast to the previous studies, Walker et al. (1987) found no relationship between size and survivorship in either male or female *Ae. triseriatus* in a mark-release-recapture experiment involving 2 size groups, large and medium. They did note a positive relationship between the size of the females recaptured and the rate at which they were recaptured, as did Haramis (1985).

Another way of looking at the question of a

size-survivorship correlation is to compare the sizes of females collected at various physiological ages. If size were advantageous to survival, the longest mean wing lengths would belong to the oldest females. Our data did not demonstrate such a trend. The predicted size of emerging females was significantly larger than host-seeking females collected in the same year ($t = -8.60$, df = 571, $P < 0.00001$). Four possible reasons are: 1) the tree holes sampled did not produce equally small females, 2) large host-seeking females were collected at a lower rate, 3) increased size is disadvantageous in early adult life, and 4) the regression equation was inadequate for the smallest pupae collected. Similar results are seen in Table 3, in which the longest wing lengths are from the mosquitoes which were collected as pupae and allowed to emerge in the laboratory. All other reports are from mosquitoes collected as adults. The large averages obtained by Haramis (1985) and McCombs (in Haramis 1985) may have resulted from: 1) differential sampling (pupae were collected from favorable larval habitats) and/or 2) increased adult mortality occurring with increased size. Among host-seeking females in our study in 1985, there was no significant difference between wing lengths of nulliparous and parous females. In 1986, a significant decrease was found in the wing lengths of the "older" parous females when compared to those of nulliparous females. Among the ovipositing females, there were no significant differences in the mean wing lengths of uniparous, biparous, triparous, and quadriparous or greater females in 3 of the 4 years studied; the only significant increase in size in older females was found between uniparous females and biparous females collected in 1985 (Table 1).

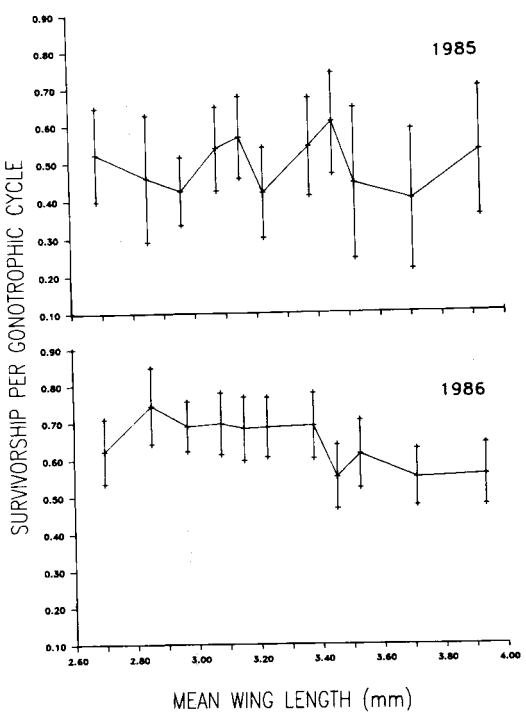

Fig. 3. Survivorship of field-collected, host-seeking *Aedes triseriatus* of various sizes (mean ± 95% confidence intervals).

Nasci (1986b), working with *Ae. aegypti*, found significant increases in size from emerging females (collected as pupae) to host-seeking nulliparous females to host-seeking parous females. He pointed out that the collected pupae might have developed in a less suitable habitat than the habitat from which the host-seeking females emerged.

Finally, our data do suggest that extremely small mosquitoes may have a decreased probability of survival and completion of a given gonotrophic cycle. The smallest uniparous individual was 2.18 mm, while the smallest females that were biparous, triparous, or quadriparous and greater were 2.55, 2.85, and 2.92 mm, respectively (Table 1). This would suggest that the smallest size class would have a diminished survivorship; this was true in 1986 though not in 1985 (Fig. 3). An alternative hypothesis that, in general, the larger mosquitoes are the first to emerge (Fig. 2) and thus are the most likely to complete multiple gonotrophic cycles would also explain these findings.

LaCrosse encephalitis epidemiology. During the period of this study, 1982–86, there were 71 confirmed cases of LaCrosse encephalitis in Wisconsin with known onset dates reported by the Wisconsin State Laboratory of Hygiene. The majority of these cases occurred in August and the first 2 weeks of September. This is the period in which small-sized mosquitoes are most common in the field, but, of the 1,768 host-seeking mosquitoes during this period, only 214 (12.1%) were of the small class.

Patrican and DeFoliart (1985) noted that small females, despite their significantly higher transmission capabilities, produced only 85% as many eggs per gonotrophic cycle as large females. In evaluating the ability of a female to produce infected progeny, the enhanced transmission capabilities of small females thus appears to be initially negated by their reduced fecundity. Patrican and DeFoliart (1985) also found in a laboratory study that the length of the gonotrophic cycle was not significantly different between small and large *Ae. triseriatus*. In addition, we were unable to demonstrate a diminished ability to obtain a bloodmeal by smaller mosquitoes, for the size distribution of partially engorged females was found to be independent of their size (chi-square value = 10.39, df = 13, $P > 0.25$). This, coupled with our

field data, which failed to demonstrate a reduced survivorship in smaller mosquitoes, indicates that the length of infective life is probably not affected by the size of the adult female. A question remains, however, as to whether feeding behavior may be affected by size. To our knowledge, this has not been studied in *Ae. triseriatus*.

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